WILDLIFE

Chapter 5

The fittest survive

From the study of fossils, we know that Yellowstone has been home to very nearly the same assemblage of mammals for at least the past 2,000 years, during which several major fire events similar to those of 1988 occurred. This continuity suggests that the park's wildlife has not been significantly affected by fires over the long run, although conditions that favor one species during one year may change the next. Twelve years after the fires of 1988, the only animals for which there is evidence of a population decline as a result of the fires are moose and snails, but only a small number of species has been studied for possible impacts. For example, although annual survey counts suggest that the fires had little or no effect on the Yellowstone bison herd, much less is known about the number and distribution of black bears, whose population is far more difficult to estimate.

Foraging While Yellowstone Burns

Extensive fires cause habitat alterations and may displace animals from their customary ranges, but they do not kill significant numbers of wildlife. Except under the most extreme conditions of fast-moving fire fronts, most appeared indifferent to the flames and, like human grazers at a 1950s cocktail party, many continued their foraging activities even in thick smoke. Yet although Yellowstone's wildlife has had thousands of years to adapt to fire, helicopters are still an alien presence. When a noisy chopper came near ferrying a water bucket or fire crew, elk visibly tensed and sometimes bolted.

One radio-collared grizzly bear ushered her two cubs around the edge of an approaching fire storm and left the area, traveling more than 20 km during the next 12 hours. But some animals appeared curious, approaching a fire and watching trees burn; a black bear was seen sticking his paw into the flames of a burning log. Another female grizzly remained in the path of the fire storm and foraged in the burned area for several days.

Bull elk, August 1989.

Why did the bison cross the road?
One of the many questions not answered by researchers in Yellowstone.

As soon as the fires began to subside, extensive surveys by foot, horseback, and helicopter located 261 carcasses: 246 elk, 9 bison, 4 mule deer and 2 moose.[1] Although this count probably included all of the large groups of carcasses, which were conspicuous because of the scavengers they attracted, isolated carcasses may have been missed. Even assuming a large undercount, the number of mortalities would be insignificant relative to the size of these animal populations and the thousands that die during a typical winter.

All of the carcasses were found in sites where the fire fronts were estimated to have exceeded 2 km in width and 4 km/hr in rate of advance. Most of the elk fatalities occurred on the Blacktail Plateau when part of the herd was trapped by a flank of the North Fork fire. Based on the presence of soot below the vocal cords, the cause of death in 26 of the 31 examined carcasses was assumed to be smoke inhalation.[2] Only two of these animals, one elk and one bison, showed clear evidence of having died as a result of burns. Examinations of the other three carcasses were inconclusive because the tracheal lining was completely burned, which could have happened after the animal had died from some other cause. One elk was euthanized because it had been severely burned and was unlikely to survive.

Most ungulate species in Yellowstone were more affected by the drought and the relatively severe winter that followed than by the fires. Although none of their winter range burned, mule deer counts declined 19% and pronghorn antelope 29% during the winter of 1988–89.[3] Park ornithologist Terry McEneaney recorded an unprecedented 80 bald eagle sightings that winter in Yellowstone, as they took advantage of the scavenging opportunities.

Elk and Bison

After studying the population dynamics of elk and bison in Yellowstone over a 15-year period, Mark Boyce of the University of Wisconsin and Evelyn Merrill of the University of Wyoming had found that three factors accounted for most of the year-to-year variation in growth rates: summer forage quality, winter severity, and population density.[4] They expected that the greatest impact of the fires on ungulates would therefore be on the quantity and quality of forage available to them in subsequent years.

Mortality after the fires.

Although elk mortality rose to about 40% in the winter of 1988–89, the multiple confounding factors make it difficult to determined how much of this was due to reduced forage because of the fires. An estimated 21,000 elk began the winter on the northern range, about 20% of which had burned; another 1,000 elk were on the more heavily forested range in the Madison-Firehole area, of which 40% burned. But even without the fires, several factors would probably have led to high elk mortality that winter.

- **Summer drought.** Forage production was 60-80% below long-term averages on the summer range of the northern elk herd and 22% below on their winter range.[5]
- **Herd density.** When the winter of 1988–89 began, the elk and bison herds were relatively large because of the two preceding mild winters, when elk mortality was estimated to be less than 5%. Because of the large herd size and small forage production, elk and bison migrated to winter ranges in larger numbers and earlier than usual. More than half the northern elk herd left the park for only the third time since 1916.[6] A disproportionate number of the elk mortalities during the fires and the following winter were adult bulls, apparently because they preferred heavily timbered slopes where they were more likely to get caught in a fire front, and because the older bulls were less likely than the cows to migrate from their established ranges in the winter.

- **Hunting harvest.** The large migration resulted in a large elk harvest by hunters: 2,400 elk were taken in 1988 (about 14-16% of the population), compared to a 1975–90 average of about 1,000 elk.[7] A special hunt sponsored by the state of Montana also removed 569 bison that had migrated north of the park.
- **Winter severity.** Based on their differing physiologies and forage needs, Phil Farnes has developed indices of winter severity for elk, bison, mule deer, and pronghorn that combine measurements of air temperature, snow acumulation, and forage production during the previous growing season.[8] On this scale, the winter of 1988–89 was the most severe for all ungulates since at least 1982. Older animals that had been able to survive the preceding mild winters finally succumbed.

Park managers considered but ultimately turned down appeals from concerned citizens to feed the elk and other wildlife during the winter after the fires. The use of artificial feeding sites causes animals to congregate at them, increasing the spread of disease, and promotes the survival of animals that do well on the supplied food, which are not necessarily the fittest animals for Yellowstone.

Nutritional stress.

Frank Singer of the park staff worked with Glenn DelGiudice of the Minnesota Department of Natural Resources to assess the physiological status of the northern range and Madison-Firehole elk herds for three winters starting in 1987.[9] A chemical analysis of urine in snow indicated that nutritional stress among elk was relatively mild the winter before the fires and severe during the first post-fire winter; by the second post-fire winter, nutritional restriction was milder and similar to that observed before the fires.

A group of researchers led by Monica Turner and Yegang Wu, then both at the Oak Ridge National Laboratory in Tennessee, developed a simulation model to study the effects of winter severity and fire size and pattern on ungulate survival on the northern winter range.[10] Using this model, they found that fire size and pattern would have no appreciable affect during mild winters. However, when the first post-fire winter snow conditions were moderate to severe (as measured by snow depth and water equivalent), the larger the fire, the greater the ungulate mortality, with calf mortality approaching 100% in a scenario that replicated the most severe winter conditions in the last 50 years.[11] A comparison of mortality rates in the winter of 1988–89 using actual elk numbers and winter conditions indicated that elk calf mortality was about a third higher because of the fires, but overall elk mortality increased only 7%.

Coughenour and Singer developed a model that simulates ecosystem influences on plant-ungulate interactions in order to assess ecological carrying capacity (ECC). According to this model, the northern range could support a mean of 21,800 elk during the period 1968–87.[12] The amount of winter forage per area varies with summer precipitation, and the area available for winter foraging varies with snow cover. Using these measures, the ECC declined 80% in the winter of 1988–89, dropping to 4,350 elk, but less than 5% of the decline was due to the fires, which had even less effect in subsequent years.

In a study of radio-collared elk calves from 1987–90, Singer found that the number lost to predation doubled during the first summers after the fires.[13] Bears, coyotes, eagles, and mountain lions may have been searching harder for calves because other foods were less available, and the calves may have been less well hidden because about a third of their tall shrub and conifer cover had burned in the fires.

Elk near Madison River during the fires.

Elk as nutrient recyclers.

Although the loss of forage caused by late summer fires can result in high ungulate mortality the following winter, studies elsewhere in the western United States have generally shown that forage quantity and quality may be enhanced in subsequent years, making larger herds possible as a result of fires.[14] But like fire, grazing animals are themselves agents of nutrient cycling. Whereas fire removes accumulated plant litter, the removal of the standing crop by ungulates before it can die slows the accumulation of litter. Whereas fire releases the nutrients in organic material by turning them to ash, ungulates achieve a similar effect by converting plants to dung and urine, improving forage growth and quality. Fire, elk, and habitat become interrelated in a way that can make it difficult to determine which came first, the elk dung or the nutritious forage. Ben Tracy found that ungulate urine had a greater impact in stimulating above-ground production on burned soil than on unburned soil.[15]

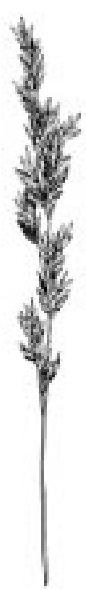
Based on patterns of plant succession in lodgepole pine, sagebrush grasslands, and sedge meadows after clearcutting or burning that had been documented in other studies, Boyce and Merrill predicted in 1989 that two fire benefits for ungulates—the increased nutrients in forage on burned sites and better foraging efficiency because the dead standing biomass and litter had been removed—would be short-lived, lasting less than three years as the fire-added nutrients were reabsorbed and dead plant litter built up again.[16] They believed the major impact of the fires on ungulates would be in the availability of various forage species, including an increase in forb diversity and production in lodgepole pine communities. The reduction in big sagebrush (*Artemisia tridentata*), which can only reestablish through seedling production, was also likely to increase the presence of more nutritious forbs on the northern range (see page 64). Boyce and Merrill expected that fire-induced improvements in forage quality would peak in 1994, but acknowledged that "we cannot know the extent to which ungulates will use the burned areas and how much better their diets will be compared to pre-fire diets."

Do elk prefer burns?

How did the fires affect forage in Yellowstone after the fires, and did these changes affect the ungulate populations? Although several studies were done during the first few years after the fires, the results were highly variable, with some researchers finding changes in forage as a result of burning and others not. While such disparities may indicate shortcomings in research methodology, they could just as well reflect the variation of ecological responses across a heterogeneous landscape. Depending on factors that may not have even been thought of yet, the forage quality at one site may improve the first year after burning, in the second year after burning at another site, and not at all at a third site of similar elevation and plant community. About the only certainty is that the removal of forest canopy in many places has resulted in more foraging areas for ungulates to choose from.

In October 1990, a group of researchers from academia and the Oak Ridge National Laboratory compared the quantity and quality of forage at 38 locations that included burned and unburned examples of four plant communities on the northern range (wet, moist, and mesic grasslands, and canopy understory). Within each community type, they found a larger quantity of biomass on the burned than the unburned site, but no differences in forage quality as measured by crude protein and digestible fiber.[17]

During two 14-week periods beginning in January 1991 and 1992, the researchers monitored grazing at 15 locations on the northern range that included burned and unburned sites.[18] They observed that from the beginning of February to mid-March 1991, elk and bison used burned areas more often than was expected based on their availability, but in 1992, they showed a preference for burned areas only during March. During the rest of the study period, elk either showed no preference or used unburned sites slightly more relative to their availability. Any nutritional advantage of feeding in burned areas where fire had reduced the standing dead and litter appeared to be gone after greenup began in the spring.



Poa sandbergii
Sandberg's bluegrass

In a two-year forage study that began in the fall of 1989 on the northern range, Frank Singer assisted Jack Norland of North Dakota State University and Lauryl Mack of the park staff in examining three grasses, two of them common in sagebrush habitat (*Agropyron spicatum* and *Festuca idahoensis*) and the other in Douglas-fir habitat (*Poa* spp).[19] Using a similar measure of forage quality to that of the previous study, they arrived at somewhat the opposite results: better forage quality at burned than unburned sites, but no increase in biomass, which actually decreased where soil heating to a depth of 5 cm was extensive. They found that the forage quality was significantly higher in the burned sites in both habitat types starting with the fall 1989 sampling; the difference was smaller a year later, but the spring forage quality was still significantly higher at the burned sites in 1991. However, other hypotheses they were testing were not borne out by their research: the diversity of elk diet did not increase; and elk did not show a preference for the burned sites, as measured by density of pellet groups.

Sometimes they don't.

Only 8 of the 20 elk that David Vales and James Peek had radio-collared in 1987 survived the winter of 1988–89, when their diets contained more indigestible fiber and lignin from trees and less grasses and forbs than in previous winters.[20] Mortality was significantly related to the animal's age and to the proportion of winter home range (as defined by each elk's movements) that had burned, which varied from 0 to 82%; 12 of the elk moved out of the home range they had used the preceding two winters. However, because there was no correlation between migration date and the extent of home range burned, Vales and Peek concluded that the early migrations in the fall of 1988 were probably due to the drought rather than the fires. The elk appeared to be using burned habitat in proportion to its availability during the summer after the fires.

Isn't forage in burned areas more nutritious?

A study of forages on the dry, relatively unproductive bunchgrass slopes of the Blacktail Plateau from 1986–90 by Frank Singer and Mary Harter, then on the park research staff, also found that the nutritional quality and digestibility of grasses were largely unaffected by burning.[21] By 1990, however, the burned sites were producing 20% more biomass than unburned grassland sites. Based on elk counts obtained during flights from 1986–91, Singer and Harter also determined that after 25% of the Blacktail Plateau burned in 1988 the portion of the northern elk herd using it for winter range dropped, from about 15% of the herd pre-fire to 8% of the herd in January 1989. When the number of elk there rose to 14% of the estimated herd size during the second and third post-fire winters, elk use of burned grassland sites relative to their availability also increased, but the elk were still showing a preference for unburned grasslands on Blacktail Plateau.

Elk avoided the burned forest sites during all three winters of the study period; the snows were deeper than in the unburned forest, and the herbaceous biomass was still 61% less in the burned forest sites during the second post-fire winter. Conifers as a food source increased from 3% to 40% of elk diets the first post-fire winter, apparently because of the reduction of other types of forage. However, pre-fire observations had shown that elk obtain less than 10% of their forage from these forested areas even when unburned, and prior studies in other locations have found that herbaceous biomass in burned forests does not rebound until six to eight years after the fires. Singer and Harter therefore suggested that greater use of burned forests by elk was more likely to be seen in subsequent years, especially during winters with below-average snow depths.

Ben Tracy found that during the first year post-fire, elk on the northern range consumed more forage at a burned site than an unburned site in the winter, but they avoided grazing in burned forest sites near Grant Village and consumed little green forage on burned northern range sites during the summer, despite their higher concentrations of nutrients than the unburned sites.[22]

Poa pratensis
Kentucky blue grass

Why Yellowstone elk may prefer unburned sites.

Based on an analysis of clippings taken at each of four sites, he determined that an elk consuming one gram of forage in early spring would ingest almost three times more minerals in a site that had burned the prior summer than in an unburned site. However, when the nutrient levels were expressed per square meter rather than per kilogram, the difference between the burned and unburned sites disappeared, causing Tracy to conclude that the nutrient concentration in burned forages was more a result of the removal of standing dead biomass than of increased nutrient uptake of soil. Tracy speculated that in both of his summer study plots, the elk may have been deterred from grazing by the presence of plants they find unpalatable: blue wild-rye *(Elymus glaucus)* in the forested sites, and a large bloom of lupine (*Lupinus sericeus*) in the sagebrush grasslands.

Singer and Harter proposed that the relatively small impact of the fires on elk forage on the northern range could be attributed to the relatively cool fire front that had quickly crossed the sites with little residual burning because of the low accumulation of litter in bunchgrass communities.[23] Nearly all of the burning on the northern range occurred during a 24-hour period beginning the afternoon of September 9, when the North Fork fire made a 34-km run. Most other post-fire studies have been done on prescribed burns, which are typically hot, slow backfires in tall-grass prairies with more litter.

Three biologists from Northwestern College in Iowa documented the changes in forage and elk use in sagebrush-dominated sites that were subjected to prescribed burning in the Custer National Forest from 1984 to 1993.[24] They found that by removing the sagebrush, the fire increased production of more preferred elk foods (grasses, sedges and forbs) and plant protein levels, rather than overall biomass. Forage quality peaked during the first year after burning, but remained above that of non-burned sites up to nine years later. The study area is part of the winter range for the northern Yellowstone elk herd, and the researchers found that elk use of the burned sites increased from 144–680%, peaking from one to four years after burning and remaining above non-burned sites for up to nine years.

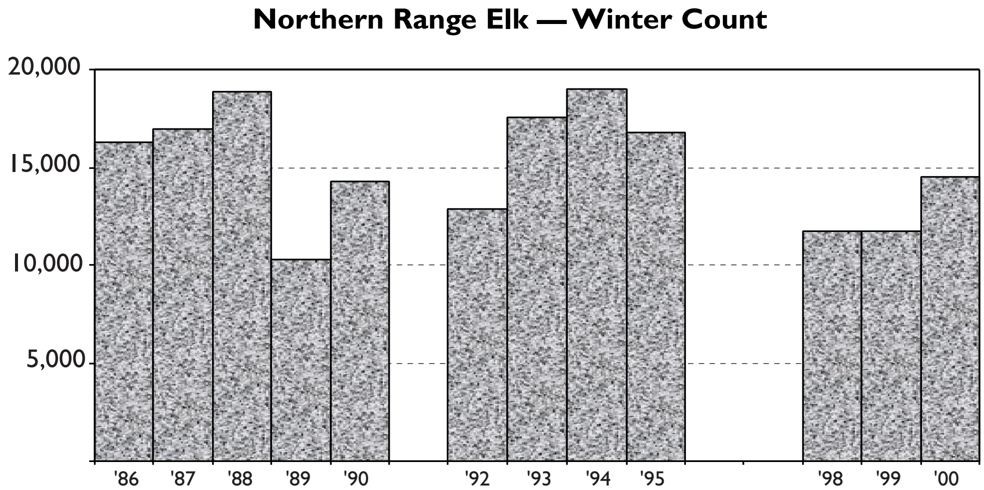
Let them eat bark.

To study the foraging habits of the Madison-Firehole elk herd, P.J.White, a doctoral student at the University of Wisconsin working under Robert Garrott, radio-collared 27 mature female elk and monitored them several times a week during the third and fourth post-fire winters.[25] The elk used the burned forests extensively for both feeding and bedding, but favored unburned areas relative to their availability, presumably because deeper snow accumulated in burned areas.

When little else is available, elk may eat lodgepole pine needles and twig tips, but live lodgepole is generally considered unpalatable because it contains large amounts of terpenes and other plant chemicals. It is generally assumed that plants produce these compounds to deter browsing. However, White and Garrott found that burned lodgepole pine bark was the third most utilized food of their radio-collared elk during the third and fourth post-fire winters, despite an apparent abundance of alternative forage, including sedges, grasses, and aquatic plants. Vales and Peek also often observed elk feeding on charred lodgepole bark.[26]

Ben Tracy collecting elk dung.

In comparing burned to unburned dead bark, a group of researchers at the University of Wisconsin found no differences in chemical composition or digestibility, but the burned bark had lower levels of the toxic compounds that serve plants as defense mechanisms against browsing.[27] The bark is lower in nutritional value then most winter forage, but the elk probably ate it because it was readily available and required little exertion to obtain. Despite their change in diet, however, no substantial declines were observed in the physiological condition of White's radio-collared elk cows; they all survived both winters, and most became pregnant and calved.

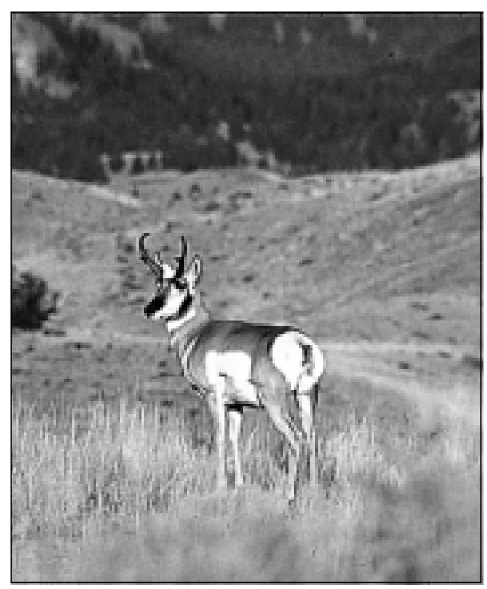


The elk population on the northern range is counted by the interagency Northern Yellowstone Cooperative Wildlife Working Group using aerial surveys.[28] Although there was evidence of a significant decline during the winter ending in 1989, that year's count (10,265) is relatively inaccurate because of poor survey conditions. In some years, no reliable counts could be made.

Pronghorn

Yellowstone's pronghorn (often called antelope) are one of the few herds that has been able to largely maintain its historic migration pattern. It was believed to number up to 2,000 in the early part of the 20th century, but was subject to culling in the 1940s and 1950s, and after dropping below 200 was estimated to be nearly 500 in the spring of 1988, and close to 600 in 1991. Since then, the herd size has declined precipitously, to a count of only 205 animals in April 2000. The reason is not known, but predation by coyotes and other carnivores, inbreeding, and loss of winter range are possible factors.

The range that is occupied year-round by about 80% of the herd, generally along the park's northern boundary, did not burn in 1988. However, from about mid-March to mid-November, the rest of the herd migrates to a higher summer range, further east in an area along the Yellowstone and Lamar rivers, much of which did burn. Based on pre-fire location data, M. Douglas Scott and Hannes Geisser concluded that the pronghorn almost always preferred non-forested range or mountain meadow habitats.[29] The most common shrub on the summer range was mountain big sagebrush, while Wyoming big sagebrush and rubber rabbitbrush dominated the year-round range.



Antilocapra americana

To determine if the 1988 fires affected the pronghorn's seasonal movements, Scott and Geisser compared migration patterns derived from historic and recent pre-fire sightings to visual observations they made along roadways and telemetry data from 73 radio-collared animals. Pronghorns were seen in at least nine unusual places in the spring and summer of 1989, eight of them entirely outside the typical pronghorn year-round or summer range, all of them in areas that had burned. These temporary shifts may have been prompted by the opening up of the forest by fire, permitting new migration routes. But such sightings had declined to one by 1993. The pronghorn did not appear to avoid using burned grasslands, probably because their preferred summer foods, forbs and grasses, quickly regrew on burned sites.

Moose

The Shiras moose, one of four subspecies recognized in North America, is a relatively new arrival in Yellowstone, having emigrated into the area sometime in the 19th century. Although apparently common in the southern part of the park by the 1880s, moose were still rare on the northern range in the first years of the 20th century.[30]

Moose habitat is often associated with forest edge and early successional stages of forest that provide conditions favorable for the growth of deciduous shrubs. Studies done in northern Canada and on the Kenai Peninsula in Alaska found that the habitat appeared to be optimal for moose within the first 30 years post-fire.[31] However, in the Yellowstone area, which has few browse species that grow tall enough to extend above the snowpack, moose must survive the winter on subalpine fir. This tree is mostly likely to establish itself under a mature forest canopy, where it faces less competition from sun-loving species and is sheltered from winter snow.

Population increase after 1900.

The increase in moose population that occurred in Yellowstone after 1900 may therefore have been a result of a closing forest canopy as well as greater protection from hunting. Based on historical records, George Gruell of the U.S. Forest Service found that the number of moose in Jackson Hole, south of the park, did not rise significantly until 60 years or more after large fires and he attributed the increase to improved winter forage.[32]

Compared to other ungulates, moose populations are difficult to estimate because moose are often solitary and occupy habitats where they are difficult to see from the ground or in the air. However, declines in hunting success outside the park led to a belief that the moose population on the northern range had dwindled since earlier in the century, and this view was corroborated by a low count in a 1985 horseback survey.

To find out more, in 1986 Dan Tyers of the U.S. Forest Service began a study of four areas of the upper Yellowstone River drainage that were known to include scattered areas of winter habitat used by moose.[33] At the time, these areas were mostly covered by lodgepole pine and subalpine fir and had varying abundance of willow stands; timber on some of the national forest land north of the park had been harvested. This research project, which continued to collect data on moose and their habitat through October 1999, was sponsored by the Northern Yellowstone Cooperative Wildlife Working Group, which includes the four agencies with management responsibilities for the northern range: the Montana Department of Fish, Wildlife and Parks, Yellowstone National Park, the Gallatin National Forest, and the Biological Resources Division of the U.S. Geological Survey.

Forage decline after the fires.

Tyers found that moose cope with winter on the northern range by seeking concentrations of food that require a minimum of energy expenditure to obtain. When the snow depth reaches about 80 cm, moose movement is restricted, and at 120–140 cm, it is nearly curtailed. Foraging efficiency, as expressed by the number of twigs browsed per meter traveled, was highest in areas with willow, but these become less accessible as winter progresses. Moose browsed most frequently on subalpine fir less than 5 m in height, which they found most abundantly in older lodgepole pine forests. Only two moose in the entire Yellowstone area appear to have died during and as a direct result of the 1988 fires,[34] but with such forests and willow stands reduced, moose have starved during subsequent winters.

One of Tyers' four study areas was not affected by the fires; each of the other three was partially or mostly burned. After the 1988 fires, the 14 moose he had radio-collared continued to be located most often in the oldest lodgepole, the oldest spruce-subalpine fir, and willow cover habitats. But the moose whose home ranges included burned areas had to increase the size of their ranges and the energy expended in foraging. Three of the moose died of starvation during the first post-fire winter, five were legally killed by hunters, and the remaining six were still alive when their monitoring ended in February 1991.

Data collected on habitat use showed that during the first post-fire winter, moose in extensively burned areas browsed on burned vegetation as well as on live lodgepole pine, which had not previously been an important food source. But overall in post-fire winters, moose depended on the remaining subalpine fir and willow, traveling less and browsing more twigs per plant compared to pre-fire. The average annual utilization of willow, as measured by the percent of twigs browsed, peaked at nearly 50% in 1989; it remained high in subsequent years but gradually declined, reaching 18% in 1997, which was close to the pre-fire average. Along with the fires and drought, this heavy browsing pressure could have contributed to willow mortality. Unlike other research on post-fire moose habitat, Tyers' study did not find an increase in shrub biomass along forest edges created by fire or logging.

Heavy pressure on willow.

To collect data on the northern range moose population, Tyers used five methods: a 177-km trail surveyed annually by horseback from 1985–99; flights conducted twice monthly from 1987–90 to locate the radio-collared moose and survey two large willow communities; daily ground observations of one willow community from April 1996 through June 1997; a survey along the 89-km road from Mammoth Hot Springs to Cooke City at least four times a month during six years from 1987–97; and eight aerial surveys conducted from 1988–92 over the general study area, concentrating on those locations where moose were most likely to be found. Although these indices of population abundance could not provide the basis for estimating the total population, Tyers believed that in combination they offered a reasonably reliable mechanism for assessing the population trend since 1985. Each method provided some evidence of a post-fire decline, with more substantial declines in areas where fire effects were more severe. For example, on the annual fall horseback survey along the Hellroaring, Buffalo Fork, and Slough creeks in an area of the Absaroka-Beartooth Wilderness where much of the moose habitat burned, the number of moose seen was 49 in 1988 and 40 in 1989, and never exceeded 20 in subsequent years.

Survival strategies.

Tyers concluded that "the loss of late successional subalpine fir patches was likely the most important reason for the decline in moose numbers" after the fires, although competition with elk for the limited availability of willow may also have been a factor. The willow on his study plots had shown some signs of recovery from the fires and drought by 1997 (see page 66), but the reappearance of forest canopies that can effectively intercept snow on winter ranges may take several hundred years. In the mean time, the moose that are surviving the post-fire winters appear to be those that can avoid excessive movement by concentrating on small islands of unburned and lightly burned habitat, or by shifting their home ranges to unburned mature conifer stands where the snow is sufficiently deep to discourage elk use.

The moose quota for the five hunting districts in Tyers' study area, which was 55 of either sex in 1986, had been reduced to 13 antlered bulls by 1998. In the first five years after wolf reintroduction began in 1995, 13 moose kills by wolves were documented in the greater Yellowstone area, 7 of them in 1999.

Alces alces shirasi

Grizzly Bears

Although relatively little is known about the number and distribution of Yellowstone's black bears, grizzly bears have been monitored since 1975 using radio telemetry because they are a threatened species under the Endangered Species Act. Most of the data presented here were collected by the Interagency Grizzly Bear Study Team (IGBST), whose representatives from seven state and federal agencies conduct research on the bear's population, food sources, and habitat in greater Yellowstone.

During the fires.

Of the 38 bears wearing radio transmitters when the 1988 fire season began, 21 had home ranges that were hit by one or more of the fires; 13 of these bears moved into burned areas after the fire front had passed, three bears (adult females without young) stayed within active burns as the fire progressed, three bears remained outside the burn lines at all time, and two adult females could not be located.[35] The bears in burned areas were observed feeding on the carcasses of ungulates killed in the fires, grazing on newly emerged sedges and bluegrass, digging in logs and anthills for insects, and excavating tubers and corms in surface burns. Examination of the carcasses suggested that when many were available, the bears ate only small portions of each, moved often from one carcass to another, and seldom buried anything for later consumption, as is done in times of scarcer food. In the 65 grizzly bear scats collected for analysis in October 1988, ungulates accounted for 28.6% of the volume, compared to an average of 7.7% in the fall samplings for 1979-87.

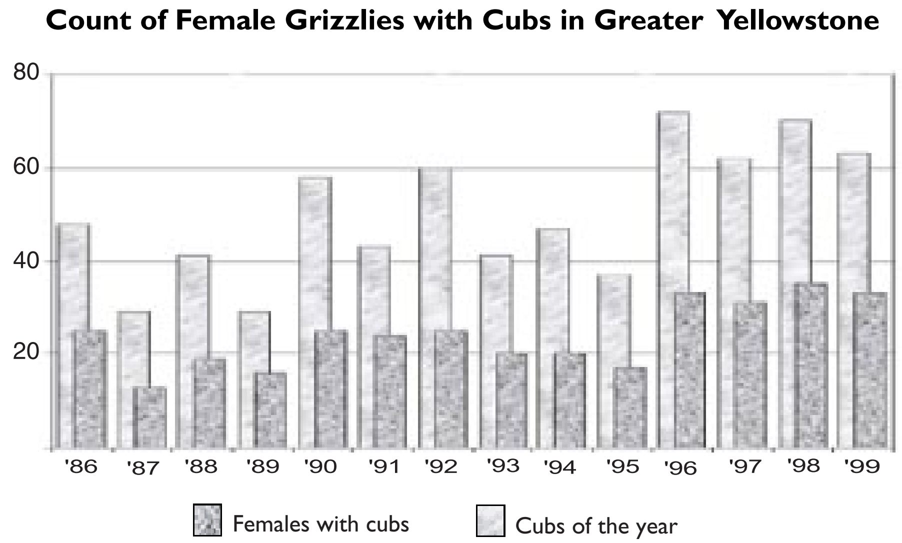
Extensive searches failed to locate the two missing radio-collared bears after fire storms passed rapidly through drainages they had been using during that summer, but one of the bears showed up in Hayden Valley in the summer of 1990, looking none the worse for wherever it was she had been. The fires had no apparent effect on the size of grizzly bear ranges, their mean rate of movement, or their choice of den sites in 1988, five of which were located in burned areas.[36] Based on 867 locations of 44 grizzly bears obtained from 1989–92, it appeared that the bears used burned habitats in proportion to their availability within their ranges. Although their annual ranges during this period were similar in size to 1975–87 averages, their seasonal rates of movement were consistently lower, indicating the adequacy of nearby food. Overall during the springs and summers of this four-year period, the bears grazed more frequently at burned than unburned forest sites, primarily on forbs, especially clover (*Trifolium* spp.) and fireweed (*Epilobium angustifolium*). But unburned forested sites were favored for feeding on ungulate carcasses in spring, insects during the summer, and whitebark pine seeds during the fall.

Post-fire grizzly diets.

The IGBST monitors the availability of ungulate carcasses, cutthroat trout, and whitebark pine seeds as three of the most important grizzly bear foods. Although there has been some evidence of a decline in the number of cutthroat spawners in certain streams since 1988, the trend cannot be clearly linked to fire impacts (see page 98). The burning of about 28% of the park's whitebark pine forest in 1988 (see page 57) could be more significant for grizzly bears. The whitebark pine may not begin producing cones until the tree is at least 100 years old, and all of the stands used by Yellowstone grizzlies to obtain the high-fat seeds were mature before the fires. Raiding cone middens buried by red squirrels, the grizzly may forage exclusively on whitebark pine seeds to the extent they are available. But because cone production varies greatly from year to year, from stand to stand, and among trees within a stand, determining its long-term effect on the grizzly bear population is difficult. Annual IGBST monitoring of whitebark pine estimates the number of cones per tree in its study transects, not the total crop size in greater Yellowstone.

Ursus arctos horribilis

However, an IGBST research project collected data from 1984–86 on the density of red squirrel middens and grizzly bear use of whitebark pine seeds in 57 line transects on Mount Washburn, a study area that encompassed the elevational range of mature whitebark pine,



(Data from the Interagency Grizzly Bear Study Team)

from 2,360 m to 2,870 m. Half of the total length of the transects burned in 1988, and the study was repeated from 1995–97, a period which had a similar pattern in average cones per tree, with a large crop preceded and followed by a small crop. Shannon Podruzny and Dave Mattson of the U.S. Geological Survey, working with Dan Reinhart of Yellowstone National Park, found no middens in transect areas that had burned. The number of active middens per kilometer had declined 27% overall compared to the pre-fire density, and the mean size of the middens had decreased 51%.[37] As a previous study had shown that bears are less likely to dig up small middens, the researchers were not surprised to find that bear feeding activity in the study area (as measured by the number of excavated middens) had decreased disproportionately, by 63%.

Fewer cones can mean more bear problems.

Since the IGBST began keeping records in 1980, years with a low cone count per tree have often been associated with more frequent grizzly bear management problems. When the bears move closer to humans in search of food, they are more likely get into trouble and have to be relocated or removed from the population entirely. However, in both 1997 and 1998, when the average cone count for all greater Yellowstone transects was fewer than 9 per tree, there were also fewer than 9 captures of "problem" grizzlies, compared to the 1980–98 annual average of 15. In 1999, when the average cone count in the park was 43, only 2 grizzly bears were captured because of conflicts with human activities.

Regardless of the fires' possible impact on the number of whitebark pine seeds, cutthroat trout, or bear captures, they have had no discernible impact on the number of grizzly bears in greater Yellowstone since 1988. The population met all three of the targets for delisting as an endangered species for the first time in 1994, and again in 1998 and 1999. As shown in the graph above, one of the targets pertains to the summer count of females who have new cubs with them. Because adult females generally have cubs every three years, the total adult female population can be estimated from this count, which is based on ground and aerial surveys. Although the species has met the recovery criteria for two consecutive years, the grizzly bear cannot be removed from the endangered species list until a strategy to secure habitat and monitor the population has been agreed upon by the various federal and state agencies involved.

Coyotes

Canis latrans

As wolves were exterminated from Yellowstone in the first decades of the 20th century, their ecological niche was partially filled by coyotes, which became the major elk predator and consumed a large portion of the available small mammal prey. Partly in anticipation of changes in the coyote population as a result of possible wolf reintroduction, Bob Crabtree and Jennifer Sheldon of Yellowstone Ecosystem Studies radio-tagged 129 coyotes on the northern range during a nearly four-year study period that began in 1989.[38] Comparing their own findings to those reported by Adolph Murie's pioneering research in 1940, they concluded that coyote territories are "traditional" and had not shifted since then, nor had the coyote's diet. Based on scat analysis, Murie estimated that 20.3% of the coyote diet was elk; Crabtree and Sheldon found 21.2%. Five of seven den areas documented by Adolph Murie in the 1940s were still being used, and the boundaries of 8 of the 12 territories located by Crabtree and Sheldon did not shift during their study period.

The proportion of each territory (averaging 15 km^2 in size) that burned in 1988 ranged from 0 to 52%, which could affect prey abundance. Ground squirrels and shrews were far more abundant in the burned than unburned sagebrush-grassland portions of the study area in 1992 and 1993, yet demographic measures such as pack and litter size appeared unaffected by burn level. However, since wolves returned to Yellowstone in 1995 (see page 85) and began killing coyotes in the battle for turf, the northern range coyote population has been substantially reduced and traditional territories abandoned. By 1998, according to Crabtree and Sheldon, "Coyote packs in this core area of wolf territories either disappeared or were in a constant state of social and spatial chaos."

Small Mammals

Small mammals are more likely to die as a direct result of wildland fires than are large mammals. The numbers involved is unknown, but rodents probably had the highest fire-related mortality of any mammal species. Although many small mammals may have escaped the fire in burrows, others probably died of suffocation as fire came through an area. Coyotes, foxes, and weasels benefitted from the loss of cover available to their prey and from scavenging on fire-killed carrion; some appeared to be attracted to fires, presumably looking for animals driven from their homes. With few islands of grass in which to hide, mice, voles, chipmunks, and squirrels became easy targets in areas of ground fire. But if the number of small mammals did temporarily decline while their predators multiplied, the increased number of predators would soon face a food shortage themselves, continuing the ongoing adjustment in the predator-prey ratio.

Roy Renkin, a biologist on the park staff, trapped small mammals for 63 days at eight burned sites beginning in September 1988 to assess immediate shifts in post-fire abundance.[39] He found that small mammal communities were not eliminated by fire, but did change in structure and habitat use. The redback vole, which is common in dense forests, was the most abundant species at the four lodgepole pine sites that had canopy burns. Renkin noted that this finding differed from post-fire studies in clear-cut areas, and attributed the difference to the density of downed trees present after fire in coniferous forests, which the redback vole appeared to favor as habitat. Fire suppression activities that use mechanized equipment and timber harvesting activities such as slash piling and burning, by contrast, alter some optimum downed log density and cause soil compaction or scarification that more adversely affects the vole than does burning. As the study period continued, the frequency with which animals were caught increased, suggesting that they were returning to forage in the burned areas.

The marten, which is considered common in Yellowstone, is known to prefer mature forests, especially during the winter. The coarse woody debris that has accumulated in such forests intercepts snowfall and creates "subnivean tunnels, interstitial spaces, and access holes" that marten use to obtain prey, escape from predators, and as thermal insulation.[40] Where trees have been removed by clearcutting, marten populations have declined, as marten seldom cross large open areas that do not have some form of overhead cover, and debris left by logging tends to disintegrate within a few years.

With some of his students, John Bissonette of the Utah Cooperative Fish and Wildlife Research Unit at Utah State University examined marten use of a 10,000-hectare site that after 1988 had a mosaic of burned, partially burned and unburned cover types, mostly lodgepole pine.[41] Based on trapping results, the area appeared to support from 25 to 57 marten. By studying marten tracks and monitoring 10 radio-collared animals in the winters of 1990 and 1991, Bissonette observed that the marten preferred areas of unburned lodgepole pine and appeared to avoid crossing open areas that were more than 100 meters wide, especially stands of canopy-burned lodgepole pine. Marten used areas of surface burn where standing trees remained as travel corridors, moving through them in a relatively straight line, without hunting or foraging, but did not prefer them over unforested areas. The critical factor in marten habitat selection appeared to be not the age of the trees, but the sub-canopy typical of old growth forests in which coarse woody debris offers access through the snowpack during the winter.

Birds

Given the variety of habitats and food sources used by different bird species, some find their options are improved after a fire, and others find they are worse. Whether Yellowstone may be considered "better" bird habitat overall as a result of the 1988 fires therefore becomes a question of whether the park can now support greater bird numbers and diversity of species, especially those species that are threatened by diminishing habitat elsewhere. Although some birds such as the boreal owl need extensive tracts of mature forest, others like the mountain bluebird require open habitats with dead trees for nesting. Burned trees may look desolate, but they are often swarming with insects that attract certain birds.

After studying seven areas in the 1960s that had burned in Yellowstone at various times in the past, Dale Taylor determined that loss of suitable habitat that resulted from the closure of the forest canopy had led to a decline in nesting birds—from 72 breeding pairs per 100 acres 29 years post-fire to no pairs 57 years post-fire.[42] Continuing his research until 1973, Taylor found that in three lodgepole pine forests on the Yellowstone plateau which had had stand replacing fires in the past, two hole-nesting species (the mountain bluebird and the tree swallow) comprised at least 30% of the breeding avifauna until the canopy closed again. Boring beetles and other insects attack the dead snags; woodpeckers concentrate in the burned area to feed on the insects and make nest holes in the snags, and abandon them each year to make new ones. Their old holes are used by other insectivorous birds that cannot make their own nesting holes, such as mountain bluebirds and tree swallows. But in Taylor's study sites, both of those species were found in much higher densities than the were the available nesting places, resulting in harassment of birds that had found nests and their occasional displacement.

Colaptes auratus
Red-shafted flicker

In 1977, Steve Gniadek, a seasonal employee at the park, set up three 300-m^2 plots near Yellowstone Lake to study fire impacts on bird species composition.[43] Two of the sites had been partially or largely burned during the preceding three years; the third site contained largely mature lodgepole pine with a dense understory of spruce fir. During 96 hours of censusing over two summer months, Gniadek found that each site was occupied by 21 species and had similar densities of breeding pairs. Of six categories of foraging birds, the largest percentage at all sites were birds that eat seeds or insects off the ground (such as dark-eyed juncos), but each site had a slightly different group of species. Only the burned sites had woodpeckers and flycatchers, while the unburned site had more species that glean seeds or insects from foliage, such as the mountain chickadee.

A comparison of breeding pairs at the burned and unburned sites suggested to Gniadek that the fires had made the habitat more favorable for 10 species and less favorable for 11 species. However, he noted that many of the species that benefitted from the fires were considered more rare or limited in range, such as the three-toed woodpecker (*Picoides articus* and *P. tridactylus*). His conclusion in 1977 was that "early successional forest represents an extremely small percentage of total forest in Yellowstone Park, and thus natural fires can be viewed as highly important in recreating a broader mosaic of vegetation types and successional stages."

Mortality during the fires.

By the time fires were on their way to creating such a mosaic in July of 1988, most of the year's new fledglings had left their nests and could escape the flames. Five bald eagle nests were destroyed in the fire, but no eagles were known to have died, and an aerial survey conducted in October and November 1988 found that territory occupancy by adult bald eagle pairs was high, indicating little if any displacement. But osprey are among the last birds to fledge in Yellowstone, and Terry McEneaney, the park ornithologist, reported that at least 17 chicks had died.[44]

Many birds received at least short-term benefits from the fires, including some osprey and other raptors. McEneaney believes they may have been alerted by the columns of smoke that signaled places were rodents were fleeing to escape the heat and flames, only to find themselves swept off the ground by some large bird. Osprey are primarily fish-eaters, but McEneaney saw one carrying a red squirrel in its talons. Although ferruginous hawks are rarely seen in the park, McEneaney saw more than 40 between Cascade Meadows and Hayden Valley on September 7, feeding on displaced voles and pocket gophers.

After the fires.

Over the longer term, the different intensities and types of burn have increased the diversity of bird habitats, with more open areas for ground nesters and dead stands of trees for cavity dwellers, and abundant insects to be found in decaying trees and litter. But it's difficult to separate the effects of these changes on birds from those of weather, which has a major impact on food availability and nesting success.

McEneaney found the greatest diversity of birds in areas where the fires were of moderate intensity, leaving a patchy mosaic of burned and unburned forest. The burgeoning crop of wildflowers increased hummingbird numbers, but in severely burned forest areas, the bark drops off trees, depriving insects of their hiding places. In these areas, even most woodpecker species were uncommon, but Lewis' woodpeckers were observed in new areas, and the hairy woodpecker can drill into a bare trunk for insects. Since plants generally take longer to reestablish in more severely burned areas, northern flickers gathering ants and American robins seeking worms find their prey more accessible.

Where fire intensities were lower, bark-chipping woodpeckers have had easy pickings, and where the trees were only swept by surface fire, the food supply for birds that forage in the canopy was not much affected. There also appeared to be an increase in cavity-nesting waterfowl such as Barrow's goldeneyes and buffleheads, and some other cavity-nesting species, including bluebirds, swallows, kestrels, and flickers.

Nucifraga columbiana
Clark's nutcracker collecting whitebark pine seeds.

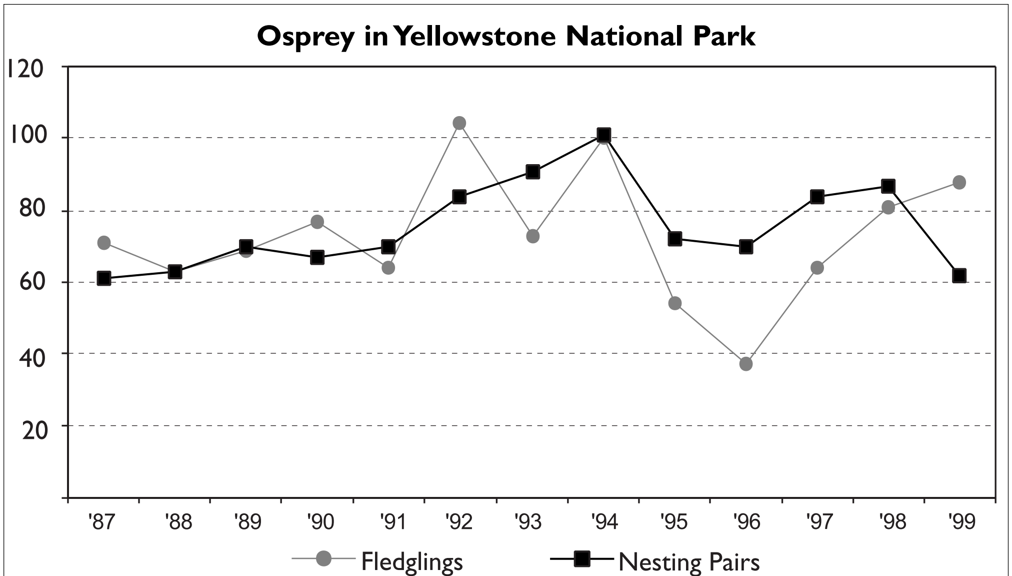
During the first two annual breeding seasons after the 1988 fires, Richard Hutto, an ornithologist at the University of Montana, Missoula, censused 34 sites in western Montana and northern Wyoming, including four sites in the park and several early successional clearcuts outside the park.[45] Like Gniadek, Hutto found that the bird species composition in recently burned forests was different from that of other Rocky Mountain cover types. Members of three guilds (woodpeckers, flycatchers, and seedeaters) were especially abundant in the burned sites. Of the 15 bird species that were generally more numerous in early post-fire communities, Hutto found five that appeared to be relatively restricted to early post-fire conditions, and one (the black-backed three-toed woodpecker) was nearly limited to the dead forests created by stand-replacement fires.

Most of the birds in burned forests relied heavily on the dead trees as food sources. Some species feed on conifer seeds (especially Clark's nutcracker, Cassin's finch, red crossbill, and pine siskin), which become more available after fire opens the lodgepole pine cones; these species peaked in abundance in the first post-fire year of Hutto's study, after which the seeds would have become scarcer. But the most abundant species were insect-eaters such as woodpeckers, which eat primarily wood-boring beetles. Hutto noted that woodpeckers responded to the increased availability of cerambicid and buprestid beetle larvae, which in some cases were themselves responding to the increased availability of unburned wood beneath the bark of fire-killed trees. Large trees were significantly more likely to show evidence of bird feeding activity than were smaller trees, which is consistent with the pattern of use by beetle larvae.[46] Aerial insectivores such as flycatchers and swallows used standing dead trees as perches from which they sallied out for their prey.

Of the 31 bird species that Hutto found nesting in burned sites, nearly two-thirds, including both open-nesting and cavity-nesting species, used standing fire-killed trees. Broken-top snags and standing dead aspen were used by cavity-nesting species significantly more often than would be expected on the basis of their abundance. From these observations, Hutto concluded that stand-replacement fires may be necessary for the long-term maintenance of bird species that are relatively abundant in or relatively restricted to burned sites. Salvage cutting may reduce the suitability of burned forest as bird habitat by removing its most important component for species that use burned forests: standing dead trees.

When the bough breaks.

But McEneaney has found the presence of so many dead trees to be a mixed blessing even for the birds that use them. Although his 1994 annual report credited the park's record high of 101 osprey fledglings partly to the "superabundance of dead snags," the drop to 54 fledglings in 1995 was "primarily due to tree instability" as a result of the fires and harsh spring weather. Similarly, he attributed the decline in bald eagle fledglings in the park from 12 in 1988 to 3 in 1989 to be "due to unstable nesting trees as a result of the wildfires," yet the fledgling count reached a record 17 in 1993 and has remained above pre-fire levels in subsequent years. McEneaney expected that falling trees during the next decade could result in egg failure, loss of nest sites, or sudden changes in nesting locations, but "these naturally occurring post-fire conditions are unlikely to cause a significant change in the bald eagle population as a whole." Two other important nesting species in the park, the trumpeter swan and the peregrine falcon, had not been affected by the fires.



(Data from McEneaney, 1999)

Invertebrates

In addition to providing a source of food for fish, birds, and other wildlife, invertebrates play an important role in many forest and grassland ecological processes, including nutrient cycling, decomposition, and seed dispersal. Tim Christiansen of West Virginia University and Robert Lavigne of the University of Wyoming found that changes in the abundance and distribution of insects and other terrestrial invertebrates as a result of the 1988 fires depended on burn intensity.[47] Some insect species benefit from the fires, especially those that could invade fire-damaged trees (see page 53). But unlike reptiles and amphibians, which typically burrow into the soil or find moist areas in which to protect themselves from fire, litter-dwelling invertebrates may decline significantly where the forest floor burned.

A bug's eye view of litter.

Nature's litter includes the dead leaves, twigs, logs, fungi, and bacteria that help provide nutrients to the soil and keep it from drying out. Starting a year after the fires, Christiansen and Lavigne compared insect communities in forest and sagebrush grassland sites, both burned and unburned.[48] Although most of the invertebrate species they found in forest stands were different from those found in sagebrush grasslands, most of the species overall were mites (Acari) and springtails (Collembola). Based on the Shannon-Wiener Diversity Index, a commonly used measure of biodiversity, they found higher invertebrate diversity in forest stands (a total of 134 species) than in sagebrush-grasslands (60 species), and greater litter diversity overall in Yellowstone than in similar habitats elsewhere in Wyoming. Consistent with Taylor's findings on the diversity of mammals and birds (see page 50), Christiansen and Lavigne recorded the highest insect diversity in middle-aged lodgepole pine stands (30 to 60 years old), and the density of insects decreased as the density of standing dead trees increased.

To compare burned and unburned forest stands, Christiansen and Lavigne collected litter and ashen material every 10 days from 12 sites from July until mid-September 1989, and from late May until mid-October 1990. Overall, the burned sites contained significantly lower litter weight, percent herbaceous cover, and density of seedlings, saplings, and log debris density than did the unburned sites, and consequently had lower densities, richness and diversity of invertebrate species. One year after the fires, invertebrate diversity was 63% lower in severely burned stands than in unburned stands, and it had increased only slightly by 1990. Density was 77% less, and the invertebrate predator:prey ratio fell from 1:24 to 1:8. However, the severely burned forested sites had significant higher seedling density and herbaceous cover than lightly disturbed sites, and higher insect density. In severely burned sagebrush grasslands, the invertebrate communities were almost completely wiped out by the fire, with diversity declining 90% and density declining 94%.

Dorothy Beetle

Their analysis suggested that certain minimum levels of herbaceous cover, tree seedling density, litter, and fallen trees were necessary to support high densities of mites and springtails. After measuring the litter at their study sites in grams per square meter (g/m^2), Christiansen and Lavigne concluded that it took at least 100 g/m^2 to accommodate abundant millipedes, which are important litter decomposers in coniferous forests, and 70 g/m^2 for high densities of ants, which help spread seeds and create pores in the soil which permit better water penetration. Post-fire reestablishment of an invertebrate community was detected with a minimum of 10% herbaceous cover, 10 pine seedlings per square meter, and 14 logs per square hectare, but many species that were abundant in unburned habitats were observed only occasionally in burned sites even two years after the fires.

Searching for snails.

Aspen groves provide habitat for snails that convert leaf litter and fallen logs into soil nutrients, and are themselves eaten by small mammals and birds. Dorothy Beetle, a retired planetarium director who undertook a five-year study of snails in aspen sites representing a range of burn intensities, identified 21 land snail and 2 freshwater species.[49] In 1989, all of the species could be found in unburned sites, but burned groves held a only a few live species and fragments of others. From 1990 to 1991, snail populations had declined somewhat even where mature aspen had survived; no new species were present, nor was there any evidence of migration into burned groves.

The land snail glides over a mucus trail it secretes using the muscular contractions of its foot. Its small size allows for some passive dispersal by wind or heavy rains and, under favorable moisture conditions, small snails may climb into the hair of mammals or feathers of birds and move to a new habitat. But snails on their own are very slow, and unlikely to survive travel across a pine forest or grassland to another aspen grove. By 1994, after two dry years, many aspen had died without replacement and snails were no longer present in any of the burned sites.

For information about aquatic insects and other invertebrates in streams, see page 96.

Amphibians

The cause of the apparent decline of amphibian populations in many places throughout the world remains undetermined. Climate changes that have increased ultraviolet radiation, whether or not contributed to by human activity, are thought to be one possible explanation. But in Yellowstone, as in most places, the lack of long-term data on amphibian populations has made it difficult to determine which species, if any, have declined, and what factors may be involved. Replication in the mid-1990s of a survey conducted in the mid-1950s in a 28-hectare area near Lake Lodge has provided Charles Peterson of Idaho State University with evidence that the spotted frog population may have declined 80%, from approximately 1,500 to 300 frogs.[50] However, comparisons of burned and unburned sites made from 1989 to 1993 suggest that the occurrence of some common species of frogs, toads, salamanders, and snakes was not significantly altered by the fires.[51]

Wolves

Now that the fires are finally going out, how about letting some wolves in?

Amidst complaints about park mismanagement and the $120 million spent on fire suppression, on September 9, 1988, Congress approved a public lands spending bill containing $200,000 for a study that would ignite another controversy about Yellowstone: the possibility of reintroducing wolves. What could have seemed less likely?

Yet less than seven years later, after extensive research into the possible consequences and dozens of public hearings, 14 wolves from Canada were released in Yellowstone. Like the reintroduction of a natural fire regime, the return of wolf packs more than 60 years after their extermination in the park was primarily motivated by the goal of maintaining as many of Yellowstone's original components and processes as possible.

Those wolves and their descendants, numbering more than 120 by the summer of 2000, have surely been affected by the changes in the landscape wrought by the fires. Although no one has studied the question, research on related topics suggests possible correlations. Wolves don't eat burned bark, aspen sprouts, or ash-enriched forage, but they do prey on elk and other animals whose abundance, distribution, and nutritional health depend partly on their consumption of such items. And a wolf pack's success in bringing down a winter-stressed elk could depend on the wolves' superior maneuvering skills in the deeper snow pack of a forested area that lost its canopy a decade before.

Canis lupus